TITLE: GLOBEC. TROPHIC RELATIONSHIPS OF JUVENILE SALMON IN COASTAL WATERS OFF OREGON AND CALIFORNIA: TOP-DOWN OR BOTTOM UP CONTROL?

PRINCIPAL INVESTIGATORS: Dr. Richard D. Brodeur

Northwest Fisheries Science Center

2725 Montlake Bvld. E. Seattle, WA 98112-2097

Ph: (206) 860-3351 FAX: (206) 860-3267

E-mail: Rick.Brodeur@noaa.gov

Dr. Thomas C. Wainwright

Northwest Fisheries Science Center

Fishery Resource Analysis and Monitoring Division

2030 South Marine Science Drive Newport, Oregon 97365 USA

Ph: (541) 867-0435 FAX: (541) 867-0389 E-mail: thomas.wainwright@noaa.gov

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STUDY PERIOD: Five Years; 1 October 1999 - 31 Sept 2004

(signature and date)
Dr. Linda L. Jones
Deputy Director
Northwest Fisheries Science Center
Seattle, WA 98112-2097

PHONE: (206) 860-3200 FAX: (206) 860-3217 Linda.Jones@noaa.gov (signature and date)
Dr. Richard D. Brodeur

Northwest Fisheries Science Center Seattle, WA 98112-2097

PHONE: (206) 860-3351 FAX: (206) 860-3217 Rick.Brodeur@noaa.gov The Northwest Fisheries Science Center, National Marine Fisheries Service, is part of NOAA, a Federal Government agency.

TITLE: GLOBEC. TROPHIC RELATIONSHIPS OF JUVENILE SALMON IN COASTAL WATERS OFF OREGON AND CALIFORNIA: TOP-DOWN OR BOTTOM UP CONTROL?

PRINCIPAL INVESTIGATORS: R.D. Brodeur, T.C. Wainwright, R.L. Emmett,

K.C. Jacobson, W.T. Peterson Northwest Fisheries Science Center Hatfield Marine Science Center

Newport, OR 97365

COLLABORATORS: C.A. Morgan

Cooperative Institute for Marine Resource Studies

Oregon State University Corvallis, OR 97331

TOTAL PROPOSED COST: \$

BUDGET PERIOD: Five Years: 1 October 1999 to 31 September 2004

PROJECT SUMMARY

We propose to study the upper-level (zooplankton, fish, birds, mammals) trophic structure and dynamics of the California Current System (CCS) pelagic zone, with a focus on the production and survival of key species such as salmonids. General effects of climate variation on biological processes in the CCS are well-documented, but few studies have focused on the processes linking physical changes with changes in the population dynamics of species in the upper trophic levels (tertiary production and above). To effectively study these linkages, empirical data and models describing the trophic structure and seasonal/interannual changes in that structure are needed.

Ocean survival of salmonids from Northwest rivers has declined markedly in the last 20 years. Although it is unclear whether ocean mortality of salmon is concentrated or evenly distributed over the entire marine life stage, there is evidence that the time period shortly after ocean entry is a critical period. While the factors causing this poor survival are uncertain, predation by large marine fishes (e.g., hake and mackerel) is suspected to be a principal source of mortality. Factors potentially affecting marine survival of salmon include specific timing of ocean entry and distribution and abundance of marine fish predators and forage fishes in the nearshore marine habitat. We hypothesize that the marine fish community has changed since the 1980s, is directly or indirectly affecting salmon ocean survival, and is structured by physical

oceanographic characteristics and that the distribution and abundance of the nearshore marine predator and forage fish community affects the amount of predation on juvenile salmonids.

We propose to characterize, over a 5-year period, the temporal and dynamic nature of the trophic relationships within the pelagic fish community during the spring-summer transition (peak salmonid migration period) and relate these dynamics to salmonid survival. A primary focus will be identification of the strength of trophic linkages between forage and fish predator species, and the influence of these relationships on predation rates on juvenile salmon. Comparisons will be made between prey availability, diet, and food consumption for the same salmon species along a latitudinal gradient. In coastal environments, the importance of mesoscale features, such as riverine plumes, eddies, and coastal jets relative to the coastal ocean as a whole will be assessed. This will require detailed comparisons of juvenile salmon, their predators, and prey between these locations and at reference sites. We propose to analyze parasite communities of both juvenile salmon and their potential predators to gain an understanding of long-term trends in host feeding, the partitioning of food and habitat, and ontogenetic shifts in feeding.

We further propose to develop a formal, empirically-based description of food-web structure in the CCS, then estimate trophic dynamics for seasons/years with adequate data, and finally to develop a multi-species population model of the CCS and apply the model in testing hypothesized linkages with lower trophic and physical processes. In particular, the model will be used to identify the relative importance of marine food-web processes (food supply, predation, competition) in controlling salmonid population dynamics, with particular focus on defining the magnitude of potential predation rates by piscine, avian, and mammalian predators. This project will interact with several existing GLOBEC projects, as well as other research projects in the CCS area.

PROJECT DESCRIPTION

1. STATEMENT OF WORK FOR THE FIRST YEAR:

During the first year of study, we plan to coordinate and take part in field sampling planned for May and September. This will involve getting supplies for the collection of stomachs and parasites as well as zooplankton. Once collected, the samples will be brought into the lab and dissected for stomachs and parasites.

First year work on the modeling component will consist of describing food-web structure for the system from literature, compiling existing data on standing biomass and bioenergetics for major food web components, then incorporating this information into a trophic flux estimate. Subsequent work will refine this model on the basis of information from GLOBEC field studies, extend the flux model to a full multi-species dynamics model, and apply the model to describe the community-level changes expected from hypothesized physical-biological linkage mechanisms.

2. RELEVANT RESULTS FROM PRIOR SUPPORT:

M. Schiewe, E. Casillas, W. Peterson, A. Baptista, D. Jay, W. Pearcy and J. Fisher. "Ocean survival of salmonids relative to migrations, fish health, predation and oceanographic conditions in the Columbia River plume and adjacent coastal waters". Bonneville Power Authority. Project #9063.

Juvenile salmon and other pelagic fish were sampled with a Nordic 264 pelagic rope trawl (15 m high x 30 m wide mouth, 200 m long) along eight transect lines on the continental shelf off Washington and Oregon during two cruise (June and September) in 1998 using a chartered fishing boat. At each station, we made a CTD cast, took water samples for chlorophyll and nutrient analysis, and sampled zooplankton with a 1/2 m 202 Fm mesh net towed vertically from 100 m to the surface, a oblique tow from 0-20 m with a 1 m 333 Fm net and a neuston tow with a 1 m² mouth and 333Fm mesh net. We captured a total of 43 juvenile coho and 242 juvenile chinook in June and 30 and 215 juveniles respectively in September. All salmon were found only on the shelf; in June all salmon were within the 13EC isotherm; in September all were within the 14EC isotherm. Over 25 different nonsalmonid fish species were caught in the surveys. The most abundant fishes in both cruises were sardines, herring and white-bait smelt. Analysis of the juvenile salmon is presently underway including stomach contents, growth (from otolith and scale analysis), and fish conditions based on several biochemical measures. Proportion of zooplankton species in the stomachs will be compared to catches in plankton nets to determine the degree to which juvenile coho and chinook salmon feed selectively.

3. INTRODUCTION

Most anadromous salmonid populations along the west coast of the United States (excluding Alaska) have exhibited general declines over the last few decades (Nehlsen et al. 1991), with regional north-south and coastal-inland patterns in degree of risk (Kope and Wainwright 1998). These patterns suggest that both freshwater habitat condition and mesoscale climate patterns affect population status, an idea supported by other work (e.g. Lawson 1993). A dramatic example is the population trends of coho salmon along the Oregon coast. Naturally-spawning populations along the coast north of Cape Blanco have exhibited a strong decline in pre-fishery adult recruitment, while spawner abundance has (until the last two years) remained fairly stable because of continual reductions in harvest rate (Fig. 1, upper panel). Comparing the downward trend in recruits per spawner (three years earlier) for natural fish with the essentially parallel trend for hatchery-produced jacks (2-year-old male salmon) per smolts released provides evidence of the importance of early ocean survival in population status (Fig. 1, middle panel). Hatchery smolts spend little time in freshwater, and jacks return after only ca. 6 months at sea, so the latter trend is likely to be largely driven by ocean conditions within a few months of ocean entry. Returns of hatchery jacks in this area is strongly correlated with adult recruitment, suggesting that the same factors affect both similarly. The trend in recruitment north of Cape Blanco is in sharp contrast to that for the Rogue River coho salmon population (Fig. 1, lower panel), which shows fluctuations in recruitment without an obvious long-term trend. Note also that here recent reductions in harvest rate have resulted in increased spawning escapement, in contrast to the pattern further north. This north-south difference in population trend adds further to the suggestion that mesoscale climate patterns are major drivers of salmonid population

dynamics.

There is presently some debate as to whether food limitation or predation limits the populations of early life stages of fishes (Leggett and DeBlois 1994). McQueen et al. (1986) showed in freshwater systems that lower trophic levels are affected most by limitations in food availability (bottom up) whereas higher trophic levels are controlled predominantly by predation (top down). In the ocean, it had been long accepted that bottom up control was most important, but this has come under increasing scrutiny by new evidence of top down control (Bax 1998). Undoubtedly, both processes operate simultaneously and may act to stabilize ecosystems. It is presently uncertain whether 'bottom-up' or 'top-down' processes, or some combination of both, limit salmon production in estuarine and nearshore coastal environments (Pearcy 1992). This is one of the most challenging areas in salmon research (e.g., Perry et al. 1998; Pearcy et al. In press) which will require a concerted effort to make substantial gains. Juvenile salmon occupy a key position in the coastal ecosystem in that they represent a trophic link between zooplankton and higher level predators (Brodeur and Pearcy 1990). Although not as numerous as some other pelagic species, they grow at a rapid rate and consume large quantities of zooplankton and small fishes (Brodeur et al. 1992). They in turn may become food for a diverse array of predators, including piscivorous fishes, seabirds and marine mammals (Emmett 1997).

4. RELATION TO PRESENT KNOWLEDGE:

There is a substantial amount of information on what prey salmon consume in marine waters (Peterson et al. 1982; Brodeur and Pearcy 1990; Brodeur 1990) and how their diet varies in relation to oceanographic conditions (Brodeur and Pearcy 1992). These studies have shown that salmon diets vary substantially depending on local (Brodeur 1989; Perry et al. 1996) and large scale (e.g. El Niño) environmental conditions (Pearcy et al. 1985; Brodeur and Pearcy 1990; 1992). However, there is only a limited amount of information on salmon prey selectivity, feeding rates, and overall food consumption relative to available food resources (e.g., Wissmar and Simenstad 1988). Accurate estimates of food consumption and growth potential have required the combination of field and laboratory data providing useful inputs to spatially-explicit bioenergetics models (Brodeur et al. 1992; Perry et al. 1996; Rand et al. 1997).

[add: disc. of hypothetical food web]Research indicates that ocean survival of salmonids is evidently determined very early during their ocean residency, with predation thought to be a major influence on salmonid ocean survival rates (Fisher and Pearcy 1988; Pearcy 1992). Although knowledge is accruing on the freshwater and estuarine predators and competitors of juvenile salmon (McCabe et al. 1983; Fresh 1996; Emmett 1997), the ecologically important taxa in coastal waters have not been adequately identified (Pearcy 1992). In addition, we lack basic information on the abundance, food habits, and feeding rates of these competitors and predators so that their impacts on salmon populations cannot be assessed at present. It appears that marine fish predators, particularly Pacific hake, (Merluccius productus), Pacific mackerel (Scomber japonicus) and jack mackerel (Trachurus symmetricus) are becoming more abundant, arriving earlier, and staying longer in coastal waters. For example, in 1977, mackerel were rarely captured during trawl surveys off Oregon; by 1995, mackerel were abundant and commonly caught at many stations (Emmett et al. MS). During a six-year ocean purse seine study off the Northwest, Brode ur and Pearcy (1986) identified a shift in the fish community, from a

community dominated by forage fish and squid from 1979-1982, to one being dominated by predators (Pacific mackerel, jack mackerel, and dogfish shark) from 1983-1984. These piscivorous fishes may be a significant cause of juvenile salmon mortality. For example, an investigation in British Columbia found that Pacific mackerel consumed nearly all the salmon smolts released from a nearby hatchery (Brent Hargreaves, Pacific Biological Station, Nanaimo, B.C. Canada, Pers. Comm.), resulting in few returns from that brood-year release.

Parasite-host relationships are naturally and integrally linked with all aspects of fish biology. The structure of parasite populations and communities is affected by the same biotic and abiotic factors that shape host populations and their communities (temperature, salinity, pollution, predator-prey interactions and their respective distributions). Parasites not only reflect long-term trends in host feeding, but also the partitioning of food and habitat, and ontogenetic shifts in feeding or niche shifts in diet (Marcogliese and Cone 1997). Valuable information may be obtained on diet and availability of prey, habitat use, predator-prey relationships, host biogeography and host condition from parasite studies. By following these patterns through time we should observe changes in trophic interactions which relate to variations in climate, populations of predators and prey, and habitat use, all of which can affect transmission dynamics of parasites and ultimately parasite community structure. Therefore, we can use parasites to better understand the ecology of their hosts and the factors that influence host ecology.

5. PROPOSED RESEARCH:

We propose to analyze the diets of juvenile salmon, their fish competitors, and potential fish predators and more finer-scale and repeated sampling over several diel periods examining the vertical distribution and feeding of salmon in relation to prey distribution and environmental variables taken at the time of collection. The parasite fauna of juvenile salmon and their potential predators will be examined as a method of tracing past feeding history and food webs unobtainable from stomach sampling (Margolis 1965, Marcogliese and Cone 1997. Finally, these data along with retrospective data from other studies will be used to construct detailed models of the pelagic ecosystem in the CCS.

There are six major objectives to our proposed study:

- (1) conduct a broad-scale analysis of the diets of all juvenile salmon, their predators, and competitors, from fish collect along inshore-offshore transects off the coast of Oregon and northern California to examine spatial, temporal, and ontogenetic variations in diet and food consumption,
- (2) conduct a spatially-intensive study of the food environment and predator field relating to juvenile coho and chinook salmon populations, focusing on contrasting sites (Heceta Bank and Cape Blanco) sites along an oceanographic gradient (frontal region or plume) to examine biophysical correlates to feeding by juveniles and predation upon them,
- (3) make detailed quantitative comparisons of the prey type and size consumed by juvenile salmon relative to what is available in the water column (neuston and plankton) at the time of collection,
- (4) analyze parasite fauna (species composition and infestation rate) of juvenile salmon and potential predators to determine trophic linkages not identified through gut content analysis,

- (5) develop empirically-based descriptions of food-web structure in the CCS, estimate trophic dynamics for seasons/years with adequate data, and develop a multi-species population model of the CCS
- (6) apply the ecosystem model in testing hypothesized linkages with lower trophic and physical processes.

5.1 Sample Collection

This study is linked to the large-scale survey of the distribution of juvenile salmon, their food and predators and will take place in May and September of 2000 and 2002 (GLOBEC proposal by Brodeur et al). During this study, trawling will be done along transects from approximately Newport, Oregon to Eureka, California. From each trawl, all juvenile salmon, potential salmonid predators, and forage fish species will be identified, enumerated, and measured. A subsample (30 specimens) of each species will be frozen in liquid nitrogen, transported to the laboratory, and measured and later weighed to determine accurate length/weight relationships. From each trawl, up to 30 stomachs of each potential marine fish predator will be removed and preserved. A random subsample of stomachs will be taken when large catches occur.

Attempts will be made to sample the available zooplankton prey at the same time under a proposal being submitted by Peterson and Swartzman. Sampling of the zooplankton prey fields will be carried out in several ways. First, during the SeaSoar and Acoustics surveys on the Mesoscale Survey boat, estimates of zooplankton biomass will be made with the acoustics. In addition, stations will be occupied several times per day to make CTD profiles and to make 1-m² MOCNESS tows fitted with 333 µm mesh nets. The purpose of the MOCNESS tows is chiefly to identify acoustics targets. Depending upon where the salmon survey boat is located in relation to the mesoscale survey boat, we may find it necessary to sample the zooplankton from the salmon boat, particularly if we have made a large catch of fishes. In this case, zooplankton would be sampled with a 70 cm Bongo fitted with 333 µm mesh nets, with a Manta neuston net (Brown and Cheng 1981) and (if feasible from the chartered fishing vessel) a 6-foot IKMT. During the Fine Scale surveys (the GLOBEC Process Cruises) on Heceta Bank (May) and Cape Blanco (September), we will have ample wire time to carry out detailed vertically-stratified sampling of the zooplankton prey fields with a MOCNESS and plan at that time to conduct studies of diel changes in zooplankton vertical distribution at the same time as we conduct the study of diel changes in diets of pelagic fishes.

The broad-scale sampling will be immediately followed by more site-intensive sampling in areas of particular importance to juvenile salmon. This sampling will coordinated with a proposed process study of euphausiid and copepod species in relation to environmental conditions proposed by Peterson and Swartzman and data will be shared between the projects. A fine-scale grid of stations will be sampled within a 50 km x 100 km survey area south of Newport (May) and off Cape Blanco (September) using a SeaSoar and towed acoustics allowing us to look at zooplankton aggregations in relation to physical structure in 3-D. The May cruise will focus on shelf and shelf-break processes along a broad bank, Hecata Bank, off Coos Bay; the September cruises will focus on separation of the coastal upwelling jet at Cape Blanco. Similar depth-stratified zooplankton and neuston sampling will be done on these surveys preferably over several complete diel cycles at the same location.

5.2 Analytical Approach

The stomach contents of all juvenile salmon and associated nekton will be examined under a dissection scope and classified down to the lowest taxonomic and developmental stage possible following the methods of Brodeur and Pearcy (1992). Size (maximum length and width) of a subsample of all major prey will be measured using an ocular micrometer (Brodeur 1991). The damp wet weights of individual prey taxa will be measured to the nearest 0.001 gram using an electronic balance. In the analysis of predator stomachs, particular attention will be paid to the characteristics of salmon found in the stomachs. Any fish prey (including salmonids) found in predator stomachs will be measured (length and width) and compared to predator length to identify any possible size thresholds or size-selectivity. Any salmonids found (either in the trawl sampling or in stomachs) will be checked for coded-wire tag or other evidence of origin.

Gut fullness, expressed as a percentage of fish body weight, will be compared to various physical (temperature, salinity, light intensity) and biological (plankton and neuston biomass, competitor abundance) to determine factors related to feeding intensity (Brodeur 1992). Number of salmonids being consumed will be calculated by multiplying the percentage of the diet composed by salmonids in marine fish predators by estimates of the predator densities (within the study area). Predator and forage fish densities will be estimated as mean number/m³ (mean number of predators per volume of water trawled). Parasites in the body cavity, muscle, stomach, and intestine will be removed and identified to species.

The diets of juvenile salmon will be quantitatively compared to that available in both surface (neuston) and subsurface plankton tows similar to that done by Brodeur (1989). We plan to use several electivity indices since the different electivity indices are strongly influenced by sample size and the presence of rare species (Lechowicz, 1982). Between habitat and day/night differences in the gravimetric proportions of the major prey categories will be tested using a parametric Multivariate Analysis of Variance (MANOVA) procedure which determines the significance of the test statistic using a non-parametric randomization test (Somerton, 1991).

Daily ration estimates of juvenile salmon will be estimated based on the diel cycle of feeding and estimates of gut evacuation rates following the methods of Brodeur and Pearcy (1997). Diel patterns of feeding and daily ration will be estimated using the Sainsbury (1986) model as implemented by the MAXIMS program (Jarre et al. 1991) fitted to both the mean and median % BW for the diel study grouped into 3 h time intervals.

5.3 Modeling Approach

We plan to summarize from existing literature food-web structure for the system and compile existing data on standing biomass and bioenergetics for major food web components. We will then develop a trophodynamic model of the system and apply the model to estimate seasonal flux for various time periods (depending on data availability). As an initial model for the system, we will adapt the approach of Robinson and Ware (1994), which used the output of a plankton dynamics model as a driving input to a pelagic fish trophic model, resulting in a seasonally-varying pelagic trophodynamics model. During Year 1, we will use an adaptation of Robinson and Ware's plankton model that is driven by seasonal cycles in upwelling, temperature, and insolation. As more refined plankton models (GLOBEC NEP projects by Huntley and Zhou; Powell and Haidvogel, and Allen; GLOBEC NEP proposal by Peterson) are developed, these

will be incorporated as driving functions for the higher trophic levels. As concepts and data sets are improved, it is anticipated that spatial structure, fish migration patterns, and size-structure within species (see Peterson et al. (1982) for evidence of the importance of size in salmonid diet composition) will be incorporated into the trophic model to accurately describe processes affecting salmonid growth and survival. The initial application of the model will be to estimate seasonal trophic flux from data obtained during sampling cruises in the early 1980s described earlier. Those cruises resulted in good estimates of numbers of fish and a description of the trophic pathways leading to and from the dominant species (Brodeur and Pearcy 1986, 1992, Pearcy and Fisher). Following this, the model will be applied to data currently being collected as part of the BPA Columbia Plume Studies (Emmett et al. MS). Finally, as data become available from the large-scale and process studies described earlier in this proposal, we will apply the refined model to these data and make comparisons among the three data sets. This will provide comparisons of trophic structure in both space (Columbia Plume to south of Cape Blanco) and space (early 1980s vs. late 1990s and early 2000s). From these comparisons, particularly noting where along trophic pathways production may exceed consumption, we will be able to consider the conditions under which salmon production may be controlled by prey availability and/or predator abundance. The ultimate application of this work is in extending our understanding of how trophic relationships control the production of salmonids and other pelagic fishes. The full model will be used in a projection mode to study the community-level consequences of changes in physical and lower-trophic driving mechanisms, as well as anthropogenic changes in trophic structure through harvest or predator management.

6. RELEVANCE TO OVERALL GLOBEC PROGRAM GOALS AND PRIORITIES

This project directly addresses GLOBEC/NEP Core Hypothesis III concerning the control of ocean survival of salmonids. There are two over-reaching goals for the NEP studies, with four general goals. This proposal is focused on the second over-reaching goal: "To quantify the biological and physical processes that determine growth and survival of juvenile salmon in the coastal zone." Understanding of the growth and survival of any juvenile fish is impossible without understanding the trophic structure that regulates both food supply and predation risks. Only through linked field studies and model development can we quantify the biological processes regulating salmon populations and the connections of those processes to physical forcing processes. Such trophic level analysis at is lacking in all presently-funded GLOBEC NEP projects. Of the four general goals, this project addresses three: the relationship of zooplankton distributions and production to higher trophic levels, the impacts of various physical-biological processes on juvenile salmonid growth and survival, and the role of predation variability on interannual variability in salmonid populations.

One of the goals of the NEP-GLOBEC program is to understand the mechanisms by which populations respond to various forcing mechanisms which will allow us to predict how species will react to future climate changes. The northern California Current has undergone substantial changes in the plankton (Peterson 1999) and nekton (Emmett et al. MS) over the last decade, including some dramatic changes in salmon abundance. Salmon are an ideal species to use in this approach because they are sensitive to changes in their environment in a number of ways, especially in their feeding dynamics (Brodeur 1997). Fortunately, there are data on

salmon feeding in our study area in the late 1970s and early 1980s (Peterson et al. 1982; Emmett et al. 1986; Brodeur et al. 1987; Brodeur and Pearcy 1987; 1990; Brodeur 1989; 1991) as well as studies conducted for more northerly stocks (Perry et al. 1996; Landingham et al. 1998) with which we can compare. Although less complete, we also have some information on what the potential predators and competitors of juvenile salmon eat (Brodeur et al. 1987; Brodeur and Pearcy 1992). A number of studies exist on changes in zooplankton abundance and species composition and these changes will be addressed in a Retrospective GLOBEC proposal by Peterson.

7. RELATIONSHIP TO OTHER PROPOSED GLOBEC PROJECTS; COORDINATION WITH OTHER INVESTIGATORS

The work in this study will be done in close collaboration with an ongoing Bonneville Power Administration study of the Columbia River Plume immediately to the north of the proposed study area. Many of the Principal Investigators are involved with this BPA study and the propose work is conceived as both an extension and a complement to the analyses planned for the coming years as part of the BPA work. This project has components examining salmon diets (headed by Brodeur), predators (Emmett) and parasites (Jacobson) of juvenile salmon, and availability of zooplankton to salmon (Peterson and Morgan). Brodeur and Peterson are collaborators on a pending National Ocean Partners Proposal to outfit an Autonomous Underwater Vehicle with upward-looking acoustics and video cameras to survey the near-surface distribution of juvenile salmon and their prey in relation to oceanographic conditions. If funded, this vehicle would be available for the planned field work described in this proposal.

Our study will benefit from interacting with ongoing GLOBEC activities such as the Long Term Observations Program (Smith et al.), spatially-explicit IBM models for juvenile salmon (Botsford et al.), zooplankton population dynamic models (Huntley and Zhou) and lower trophic models (Allen et al.). We anticipate extensive collaboration with other proposed GLOBEC investigations. Principal among these are a proposal to examine the fine-scale distribution of euphausiids (Peterson and Swartzman), euphausiid population dynamics (Peterson), the broad and fine-scale distribution of salmon in relation to oceanographic conditions (Brodeur et al.), distribution and ecology of seabirds and mammals (Tynan and Ainley), growth and condition of juvenile salmon (Casi llas et al.), and genetic stock origin of salmon (Grant).

8. INFORMATION/TECHNOLOGY TRANSFER

A research report will be written at the end of each study year. Final results of this study will be published in several peer reviewed journal and presented at several scientific meetings or workshops. We will also disseminate information through the NMFS/NWFSC WEB site when possible.

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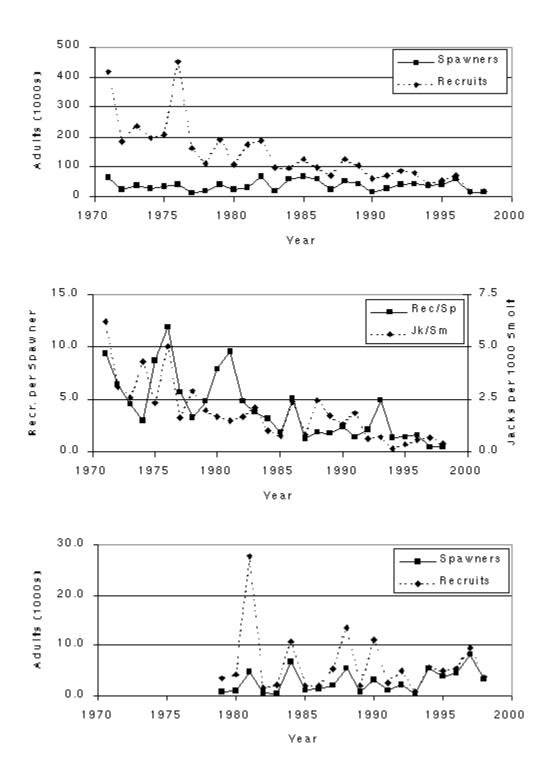


Figure 1. Trends in Oregon coast coho salmon spawners, pre-harvest recruits, and productivity. Upper panel: natural spawners and recruits north of Cape Blanco; Middle panel: natural recruit:spawner ratios (north of Cape Blanco) and hatchery jack:smolt ratios; Lower panel: natural spawners and recruits from the Rogue River. Based on data from Pacific Fishery Management Council (1999) and Oregon Department of Fish and Wildlife unpublished data.